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LARVAL TREMATODES FROM NORTH AMERICAN FRESH-WATER SNAILS

PRELIMINARY REPORT *

WILLIAM WALTER CORT
Department of Biology, Macalester College

Almost nothing is known of the life histories of the trematodes of North America. Some progress has been made in the study of the adults, but as yet there are only a few scattered observations on larval stages. During the fall of 1913 the study of the larval trematodes from fresh-water snails was undertaken by the writer at the suggestion of Prof. Henry B. Ward, as an attempt to open up this undeveloped field. The snails studied, which were obtained from several sources, yielded a surprisingly large number of species of cercariae, belonging to a wide variety of trematode groups. Fourteen new cercariae with their sporocysts or rediae were studied in detail, especial attention being given to observations on the living animals. The complete results of this work, embodying a detailed discussion of anatomy, histology and relationships, will appear shortly. The present report contains some of the more interesting observations on the structure and activity of these forms.

In the grouping of the cercariae the classification of Lühe (1909: 173-210) has been followed in most instances. In those groups in which the structure of the cercaria corresponds fairly closely to that of the adult, as in the amphistomes and the echinostomes, this classification is very satisfactory, but in those divisions where larval adaptations dominate the structure and where little is known of further development, as, for example, in the Stylet cercariae or microcercous group, the arrangement is certainly to some extent purely artificial.

Of the fourteen cercariae studied, one is a monostome, two are amphistomes and the rest belong to five different subdivisions of the distomes.

MONOSTOME CERCARIAE

Rediae and cercariae of a monostome, which I propose to name *Cercaria urbanensis*, were found during December 1913, in the livers of 5 per cent. of the full-grown specimens of *Physa gyrina* Say, from a drainage ditch near Urbana, Ill. There were present in the infected livers immature and fully developed rediae and free cercariae in dif-

* Contributions from the Zoological Laboratory of the University of Illinois, under the direction of Henry B. Ward, No. 35.

ferent stages of development. No rediae were present in which other rediae were developing and no mature cercariae remained in the rediae.

When freed from the liver of the snail the redia of this species has considerable power of extension and contraction, the immature ones especially stretching out the anterior end and reaching in all directions. No locomotor appendages were present in any stage and no locomotion was noted. In shape they are elongate sacs, smallest at the anterior end and widest in front of the posterior extremity. The intestine is voluminous, having a diameter of from one-third to two-thirds the width of the body and reaching almost to the posterior extremity.

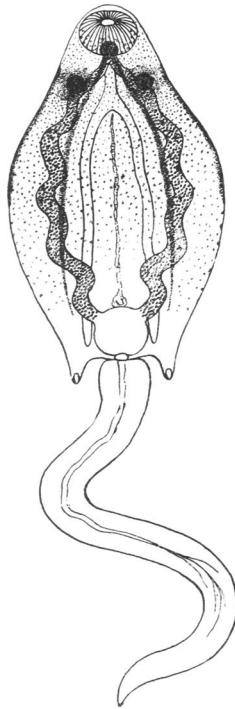


Fig. 1.—Mature *Cercaria urbanensis*, ventral view. Cystogenous glands not shown. X 140.

The methods of locomotion of *Cercaria urbanensis* (Fig. 1), either when swimming in open water or when creeping on a substratum, are very striking. The body when swimming is contracted into a round ball and the powerful tail is curled ventrad and lashes with great rapidity driving the animal with considerable speed through the water. In spite of the absence of a ventral sucker, the cercaria is able to creep by utilizing two projections which form the posterior lateral angles of the body. These projections, which are reinforced by cuticular struc-

tures, are thrust against the surface in a manner analogous to setae and aided by the oral sucker push the animal along. *Cercaria urbanensis* encysts in the open and the complete process of encystment was followed under the microscope.

The shape of *Cercaria urbanensis* is quite variable. An individual may contract until its length is 0.27 mm. and its width 0.20 mm., and it may extend itself to 0.54 mm. in length and 0.11 mm. in width. The tail changes its length from 0.20 mm. to 1.2 mm. The histological structure of this tail is very interesting on account of its adaptation for powerful movement. The structure of this cercaria agrees in a general way with that of a group of closely related monostomes of which *Cercaria imbricata* Looss (Looss, 1896: 192-197), and *Cercaria ephemera* Nitzsch (Ssnitzin, 1905, Plate 4, Figs. 75 and 76), are examples. It differs from these forms in details of structure, such as the length of the intestine of the redia and the structure of the locomotor projections of the cercaria. *Cercaria hyaloecauda* Haldeman, a monostome cercaria from North America, as described by Evarts (1880) is considerably larger than *Cercaria urbanensis*.

AMPHISTOME CERCARIAE

Amphistome cercariae are very easily recognized by the presence of the large acetabulum at the posterior end of the body. Although large numbers of adults of this type have been reported, but three cercariae are found in the literature, namely, the cercaria of *Diplodiscus subclavatus* (Goeze), best described by Looss (1892: 162-166); *Cercaria pigmentata* Sonsino, which was shown by Looss (1896: 185-191) to be the larval form of *Paramphistomum cervi* (Zeder), and the cercaria described by Looss (1896: 177-185) as the larval form of *Gastrodiscus aegyptiacus*. Of these cercariae that of *Paramphistomum cervi* belongs to the subfamily *Paramphistominae*, and the other two to the *Diplodiscinae*. My studies add to the second subfamily two cercariae, which differ from the known forms in details of structure both of the redia and cercaria.

These two cercariae were collected from specimens of *Planorbis trivolvis* Say, from three localities. Two snails out of eighteen of this species from Lawrence, Kan., and one from large numbers examined from around Urbana, Ill., contained the first of these forms, a large pigmented cercaria, to which the name *Cercaria inhabilis* is given. The second, a small unpigmented cercaria, *Cercaria diastrophia*, was found in one of twenty specimens of *Planorbis trivolvis* from a small pond in the suburbs of Chicago. In all the infected snails adult and immature cercariae were found free in the livers, the mature forms being nearest the periphery, and the active rediae contained no fully developed cer-

caria. There were no sporocysts present and no rediae in which rediae were developing.

The rediae of *Cercaria inhabilis* were all in about the same stage of development. When freed from the snail they were very mobile, extending and contracting and making some progress even on the smooth surface of a watch glass. There are present two pairs of locomotor appendages and the posterior extremity is attenuated and pointed. The pharynx is small in proportion to the size of the body and the intestine is voluminous and extends more than one-third of the distance from the anterior to the posterior ends.

Cercaria inhabilis (Fig. 2) swims sluggishly in open water. It contracts its body and lashes rapidly with its tail moving forward in an unwieldy irregular fashion. In fact, the body is too large in proportion to the size of the tail for rapid locomotion. On a substratum the cercaria extends and contracts its body, but is unable to creep with the aid of the suckers. It is the largest of the cercariae studied. In the different stages present the development of the pigmentation could be traced from little spots around the eyes until it spread through most of the body. Although cystogenous glands are highly developed, filling most of the body, none of the cercariae under observation were seen to encyst.

Cercaria diastrophia (Fig. 3) resembles *Cercaria inhabilis* in general structure. It differs from this form in the size and shape of the body, the ratio in the size of the suckers and in the position of the acetabulum, in the amount of pigmentation, and in the anlage of the reproductive organs.

The redia of *Cercaria diastrophia* is even more active than that of the former species, being able to move well with the aid of the two pairs of locomotor appendages and to stretch to five or six times its usual length. This mobility is correlated with extreme development of the circular muscles, which show clearly externally as annular rings.

The only adult trematode from North America which resembles these amphistome cercariae in structure is *Diplodiscus temporatus* Stafford. Cary (1909) described as belonging to the life history of this species sporocysts and rediae, both containing cercariae from *Goniobasis virginica* obtained near Princeton, N. J. In 1911 Cary kindly sent me some of the material used in the preparation of this paper, including specimens of *Diplodiscus temporatus* from his experimental tadpoles. A study of this material and a careful analysis of Cary's account shows that he has described as belonging to this species two entirely different types of cercariae, that is, a large gymnocephalous cercaria developing in rediae and a small xiphidiocercaria developing in sporocysts. Since in his infection experiments he used only the

larger species, he certainly can have no evidence that the smaller form has any connection with *Diplodiscus temporatus*. Therefore, Cary's whole discussion in the embryological part of the paper (1909:617-647) which is based on the study of the sporocysts and the cercariae developing in them, cannot without further evidence be given a place

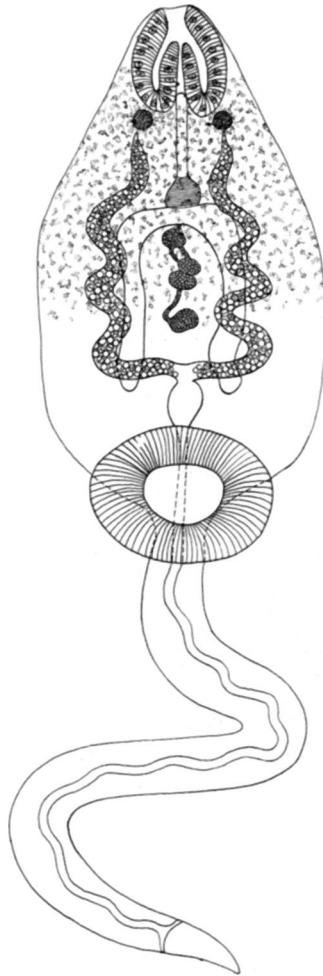


Fig. 2.—Mature *Cercaria inhabilis*, ventral view. Cystogenous glands not shown. X 88.

in the life history of *Diplodiscus temporatus*. However, it proves the thesis which Cary sets out to make that the embryo in the sporocyst develops from parthenogenetic eggs, and is therefore a very important contribution to trematode embryology. I am convinced that the larger form, which I shall call *Cercaria megalura*, is not the cercaria of

Diplodiscus temporatus, as Cary maintains, because it is so fundamentally different in structure from all known amphistome cercariae and from the adult of this species. Further, Cary's infection experiments are not sufficiently controlled to be conclusive and admit of an entirely different interpretation from the one he gives. To produce infection he puts the tadpoles into jars with snails which contain these cercariae and because the tadpoles were later found to be infected with

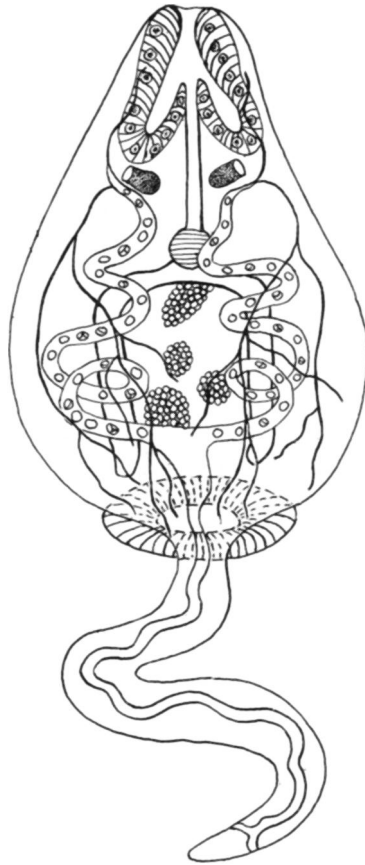


Fig. 3.—Mature *Cercaria diastrophia*, ventral view. Cystogenous glands not shown. X 176.

Diplodiscus temporatus, he concluded that these trematodes had developed from cercariae in the snails. The first adults were found one week after the beginning of the experiments. These cercariae are so fundamentally different from the adults into which Cary supposed that they developed in one week's time, that I am convinced that he is in error in his conclusions and that the experimental tadpoles, in spite of

the checks which he used, were already infected with *Diplodiscus temporatus*. Lack of space admits in this report of only the bare outlines of the conclusions in this matter. A full discussion of the data and arguments which have led to the above conclusions will be published in the final paper.

The smaller of Cary's two species of cercariae I shall call *Cercaria caryi* (Fig. 4). Since it is very small and no living material is available for study, no extended description will be attempted. It evidently belongs to Lühe's group of Cercariae microcotylae under the Xiphidio-cercariae. I was fortunate enough to obtain further material of *Cercaria megalura*, so that a detailed study was possible. Some facts concerning this form and certain corrections of Cary's description will be given here.

DISTOME CERCARIAE

The great bulk of known cercariae belong in this division. In my material were eleven distome cercariae representing five of the subgroups.

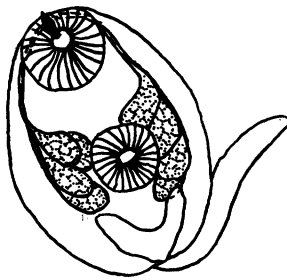


Fig. 4.—Mature *Cercaria caryi*, ventral view. From Cary's material. X 280.

Gymnocephalous Cercariae

Since beyond the fact that they develop in rediae the cercariae placed in this subdivision agree only in the absence of certain characters, it is probably an unnatural group. However, in the present state of our knowledge it is very convenient to retain it. From my material only *Cercaria megalura*, wrongly described by Cary as the larva of *Diplodiscus temporatus*, belong here.

Rediae containing cercariae of this species were found in one from seventy-three specimens of *Pleurocera elevatum* Say, from the Sangamon River near Mahomet, Ill. This species, as Cary entirely failed to note, resembles very closely in both activity and structure *Cercaria distomatosa* Sonsino, best described by Looss (1896: 197-204). These two species differ in the size and the relations of the digestive system of the redia and in the size of the cercaria and in the relations of its excretory system. Since they differ very greatly from all others of the

gymnocephalous group, I propose to make them the basis of a subgroup, to which the name *Megalurous cercariae* may be given.

The rediae of *Cercaria megalura* are very active and the region back of the locomotor appendages on account of its mobility and attenuation resembles a tail. The anterior region of the body can be extended and contracted freely and with the aid of the locomotor appendages locomotion was possible. The intestine is very voluminous, being from one-third to two-thirds the diameter of the body and reaching almost to the posterior tip.

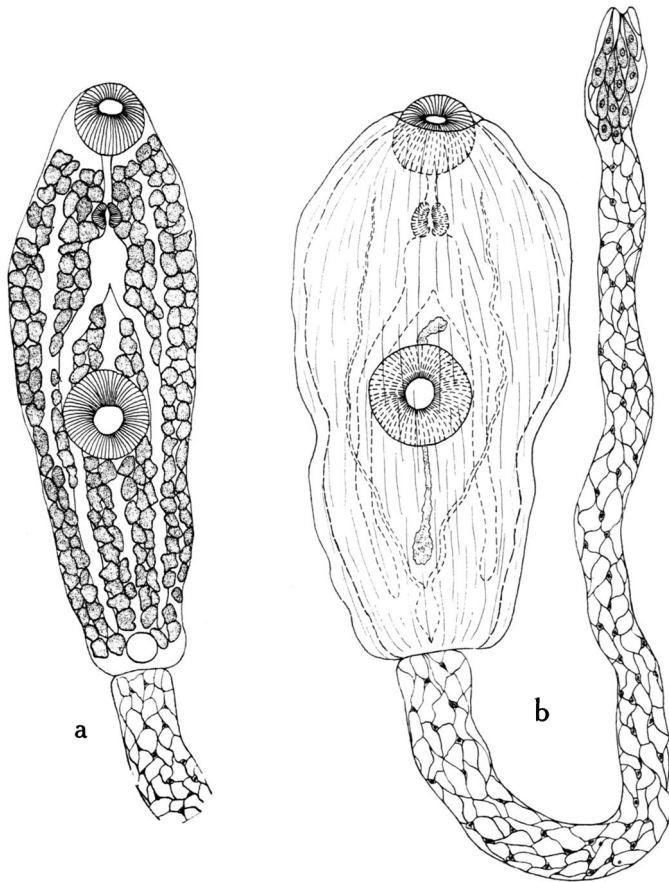


Fig. 5.—Mature *Cercaria megalura*, ventral view. (a) Before extrusion of cystogenous material. X 195. (b) After extrusion of cystogenous material. X 195.

Cercaria megalura (Fig. 5a) is unable to use its tail for swimming in open water, but on a surface creeps fairly rapidly with the aid of the suckers. At times the cercaria becomes attached by the tip of its tail which is furnished with an adhesive organ. It then becomes

extended to five or six times its usual length and is greatly attenuated. In this position it moves continually with a wriggling serpentine motion, which makes it resemble a tubificid worm. This activity probably aids in transfer to a secondary intermediate host. None of the cercariae were seen to encyst, although large numbers of them extruded cystogenous material in the form of a sort of open tube around the body (Fig. 5b).

The study of both Cary's and my own material of *Cercaria megalura* shows that he is in error in his description of the digestive system, the tail, and the anlage of the reproductive organs as is evident on comparison of Cary's Figure 6 of Plate 30 with Figures 5a and 5b of this paper.

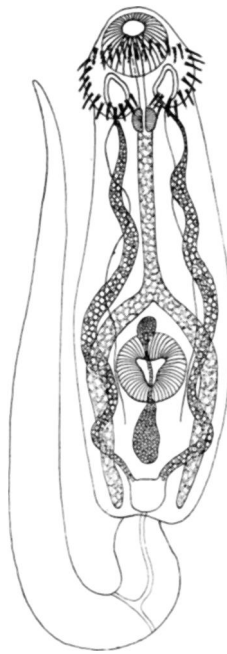


Fig. 6.—Mature *Cercaria trivolvis*, ventral view, cystogenous glands not shown. X 195.

Echinostome Cercariae

Cercariae belonging to the family Echinostomidae are very easily recognizable because of the presence as in the adult of the anterior collar and crown of spines. The structure of the excretory and digestive systems are also very characteristic for the whole group. The anterior crown of spines gives a very definite basis for comparison between larvae and adults, and many suggestions of life histories have been made on this character.

Two cercariae of this group were found in the material studied. In neither of them are the anterior spines like any of the known American adult echinostomes, and they differ in a number of points from any of the cercariae of this group described.

Rediae in which cercariae were developing, as well as encysted cercariae of the first of these species, for which the name *Cercaria trivolvis* is proposed, were found in several specimens of *Planorbis trivolvis* from Urbana, Ill. *Planorbis trivolvis* is able, then, to serve both as intermediate and secondary intermediate host for this trematode. The second echinostome species, *Cercaria rubra*, was found encysted in six out of thirty-six specimens of *Campeloma subsolidum* Anthony, from Hartford, Conn. The snail in this case is merely the secondary intermediate host.

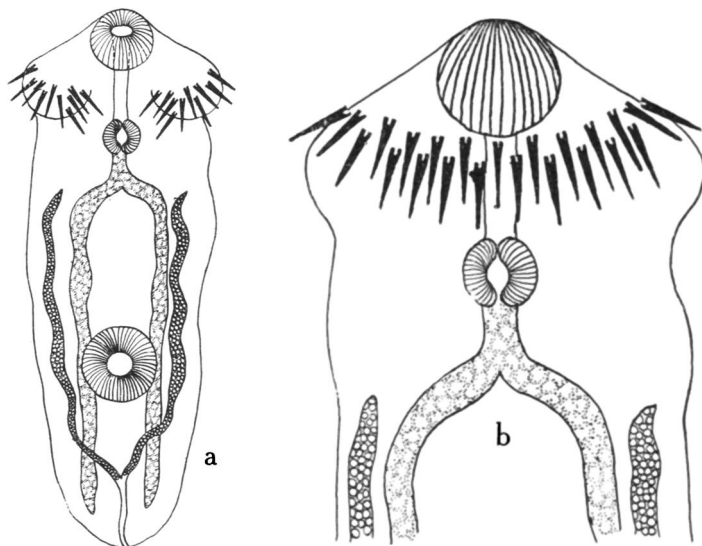


Fig. 7.—*Cercaria rubra*. (a) Freed from cyst, ventral view. X 195. (b) Anterior end of cercaria, dorsal view. X 390.

The rediae of *Cercaria trivolvis* are much like those described for other echinostomes, differing from them only in details of structure.

The cercaria (Fig. 6) of this species moves actively, both by swimming in open water and by creeping on a surface. The tail is powerful and extends when the animal is swimming to two or three times the length of the body. For the swimming movement the cercaria bends ventrad almost double, with the posterior half of the body above the anterior. The tail, which extends out beyond the anterior end, lashes vigorously and propels the animal rapidly. Of all the cercariae

observed only *Cercaria urbanensis* moved more rapidly than *Cercaria trivolvis*.

The crown of spines of *Cercaria trivolvis* consists of thirty-seven spines of equal size, arranged in two alternate rows which are broken in the middle of the ventral surface. The two or three nearest the midline on each side of the ventral surface point in. An idea of the general structure of this cercaria can be gained from the figure.

Cysts of *Cercaria rubra* were large and thick walled. The worm almost completely fills the cyst and moves only slightly. Worms were freed from the cysts and their structure studied (Fig. 7a and 7b). Most typical is the arrangement of the spines in the anterior collar. There are forty-three spines of uniform size arranged in two alternate rows. The four on each side nearest the midline of the ventral surface point inward.

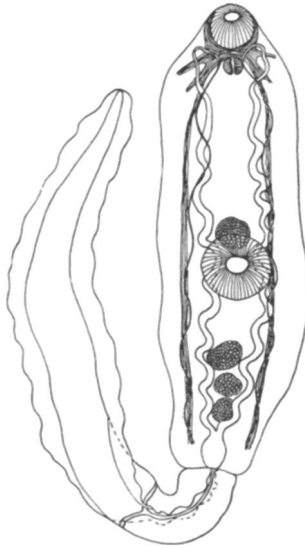


Fig. 8.—Mature *Cercaria reflexae*, ventral view. Cystogenous glands not shown. X 88.

As an appendix to the Echinostome cercariae I treat the following form: The livers of eight out of thirty-eight specimens of *Lymnaea reflexa* Say, from Chicago, contained rediae in which were developing a species of cercaria, for which the name *Cercaria reflexae* is proposed. Also in the body cavities of a number of the same snails were encysted cercariae of the same species.

Cercaria reflexae (Fig. 8) agrees with the echinostomes in the general structure of the redia, and in the method of locomotion and structure of the excretory and digestive systems of the cercaria. However,

it lacks entirely the anterior collar and crown of spines typical of the echinostomes. No record has been found of any species, either cercaria or adult, that corresponds in structure to this species.

Microcercous Cercariae

The group of microcercous cercariae includes a very heterogeneous collection. Some of them develop in rediae and some in sporocysts. Some have stumpy tails developed as suckers and some have merely blunted tails. Dollfus (1913) has already formed within this group a subdivision, the Cotylocercous cercariae, which contains a number of marine forms, centering around *Cercaria pachycerca* Diesing, with

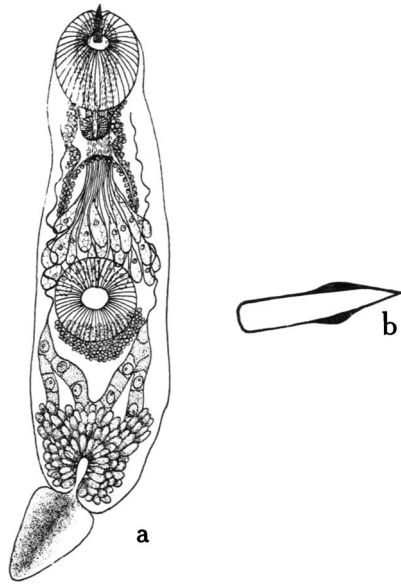


Fig. 9.—Mature *Cercaria trigonura*, (a) ventral view. X 260. (b) Stylet of same. X 866.

their tails developed as suckers. Whether there is any close relationship between the members of this group and the other forms now included within the microcercous cercariae is impossible to determine in the present state of our knowledge. It is therefore best to retain the name microcercous cercariae provisionally to cover all short-tailed forms which do not fit into other groups.

Such a cercaria was found in four out of the thirty-six specimens of *Campeloma subsolidum* from Hartford, Conn. The tissues of the body above and at the bases of the gills of these snails contained large numbers of free mature cercariae. There were also present rediae in

different stages of development in which only little differentiated germ balls could be distinguished.

This cercaria (Fig 9 a), for which I propose the name *Cercaria trigonura*, has an elongate cylindrical body and a very short heart-shaped tail. It is unable to swim freely in open water, but extends and contracts its body very rapidly. The tail bent ventrad and pushing against the substratum aids somewhat in locomotion and the oral sucker at times becomes attached. By this peculiar method the animal is able to make a little progress with a great deal of effort.

On the ventral surface of *Cercaria trigonura*, just at the base of the tail, is a slit-like opening, which extends forward a short distance and dorsad reaches up into the body. Opening into the cavity thus formed are large numbers of unicellular glands which stain very heavily with hematoxylin. The position and structure of this posterior gland suggests that it may function for adhesion. No activity which suggests such a function has been observed. Figure 9a shows the characteristic shape of the stylet of this species. The large bicornuate excretory vesicle lined with a layer of granular cuboidal epithelial cells is also characteristic.

Cercaria trigonura is unique among the microcercous cercariae in having a large posterior gland opening at the base of the tail and in its bicornuate excretory bladder. It differs from all except *Cercaria limacis* Moulinié (1856: 83, 163-164), in having a blunted tail which is not modified as a sucker.

Furcocercous Cercariae

The Furcocercous or forked-tailed cercariae are very imperfectly known. Although at least a dozen species have been reported as distinct, the anatomy of only a few of them is at all well worked out and the life history of no one of them has been determined.

Tangled masses of sporocysts containing a cercaria of this type were found in the livers of five out of the thirty-six specimens of *Lymnaea reflexa* from Chicago. The name *Cercaria douthitti* is proposed for this form. The sporocysts are long cylindrical tubes of varying caliber which are unbranched and very much tangled together. When the cercariae were freed from the sporocysts they moved around somewhat erratically by a vigorous vibration of the body and tail. The oral sucker was not fully developed, so that the creeping movement could not be accomplished.

Cercaria douthitti (Fig. 10) is a small cylindrical cercaria with eyespots and a tail considerably longer than its body. Although it has no stylet, the region back of the acetabulum is almost completely filled with eight large unicellular glands, which seem to be analogous to the

stylet glands in certain other forms. Two groups of ducts from these glands run forward along each side and pass through the oral sucker to open at the anterior tip.

Only one forked-tailed cercaria, *Cercaria ocellata* La Valette St. George (1855:22-23), resembles at all closely in structure *Cercaria douthitti*. *Cercaria ocellata* is, however, almost twice as large as my species and has fin-like projections on the divided lobes of the tail.

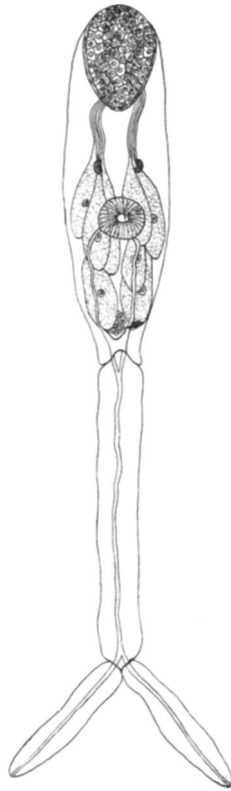


Fig. 10.—Mature *Cercaria douthitti*, ventral view. X 195.

Xiphidiocercariae

About one-third of all the known cercariae belong to the Xiphidio- or stylet cercariae. They are characterized as slender-tailed distome cercariae with a boring spine. As this group contains a large variety of forms, numerous subdivisions have been proposed. In my material are found five new stylet cercariae of four different types. Two of them are so much alike and agree so closely with several European cercariae that it is proposed to unite them into a new subgroup, which will be discussed next.

Polyadenous Cercariae

The name Polyadenous cercariae is proposed as a group designation for those of the Xiphidiocercariae which agree in the following characters.

1. Development in much elongate sac-shaped sporocysts.
2. Tail slender and except when much extended less than body length.
3. Acetabulum back of the middle of the body and smaller than the oral sucker.

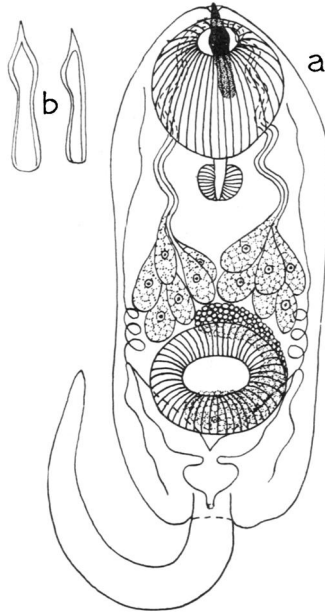


Fig. 11.—Mature *Cercaria isocotylea*; (a) ventral view. X 415. (b) Stylet of same. X 577.

4. Stylet about 0.030 mm. in length, six times as long as broad, and with a thickening about two-thirds of the distance from the base to the point.

5. Stylet glands six or more on each side between the acetabulum and the pharynx.

6. Excretory bladder bicornuate.

Two European fresh-water cercariae, *Cercaria limnaeae-ovatae* von Linstow, and *Cercaria secunda* Ssinitzin, can without question be placed in this group. I am able to add two American species, *Cercaria isocotylea* and *Cercaria polyadena*.

Cercaria isocotylea (Fig. 11a) was found in elongate, must twisted cylindrical sporocysts in 18 per cent. of 170 specimens of *Planorbis*

Some facts are known of the further development of the polyadenous cercariae. *Cercaria limnaeae-ovatae* has been assigned to *Opisthioglyphe rastellus* (Olson), and Ssinitzin (1905) suggests that *Cercaria secunda* may be the larva of a *Plagiorchis* species. It is possible, therefore, that the American forms belong to Lühe's subfamily *Plagiorchiinae*.

Microcotylous Cercariae

Lühe's group of Cercariae microcotylae contains a number of very small Xiphidiocercariae, most of which are very insufficiently known. Besides the forms listed by Lühe (1909: 196-198) and *Cercaria caryi*,

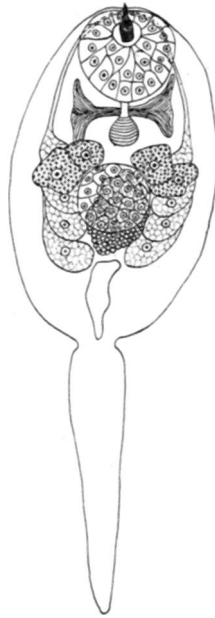


Fig. 13.—Immature *Cercaria leptacantha*, ventral view. X 433.

three Egyptian cercariae of Looss (1896: 227-232), *Cercaria cellulosa* sp. inq., *Cercaria pusilla* sp. inq. and *Cercaria exigua* sp. inq., should be placed in this group. An American species to be called *Cercaria leptacantha* is added from my material. The tissues above the gills in three of the thirty-six specimens of *Campeloma subsolidum* from Hartford, Conn., was infected with oval thin-walled sporocysts containing cercariae of this species.

The general structure of *Cercaria leptacantha* is shown in Figure 13. None of the cercariae were fully matured and but slight movement was noted.

Cercariae Ornatae

Lühe (1909:190) defines the *Cercariae ornatae* as follows: "Distome Cercariae mit Bohrstachel, deren schlanker Ruderschwanz einen Flossensaum besitzt."

In this group are placed *Cercaria ornata* La Valette, and *Cercaria prima* Ssinitzin. From my material an American form, *Cercaria hemilophura*, is added. This group must very evidently be considered as merely provisional, since the three cercariae comprising it are very different in structure, having little in common except the presence of a fin-like projection from the tail.

A tangled mass of elongate, orange-pigmented sporocysts containing cercariae of *Cercaria hemilophura* were found in one of twenty

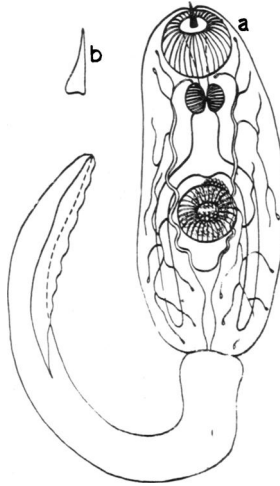


Fig. 14.—Mature *Cercaria hemilophura*; (a) ventral view. Cystogenous glands not shown. X 140. (b) Stylet of same. X 433.

specimens of *Physa gyrina* from Rockford, Ill. The sporocyst tubes do not branch and are of varying caliber. Club-shaped ends jut out from the mass and sway slightly backward and forward.

Cercaria hemilophura (Fig. 14a) is a large cercaria, over 0.40 mm in well-extended specimens, and its tail is about the length of the body. Along the ventral surface of the posterior half of the tail extends a fin-like projection which at its widest is about half the width of the tail. The stylet (Fig. 14b) is small, tapers regularly to a point and has no thickened region. The body contains large numbers of cystogenous glands, but no stylet glands could be distinguished. Other points of general structure can be made out from the figure.

A new subgroup of gymnocephalous cercariae, the megalurous or heavy tailed cercariae, is proposed; it includes *Cercaria megalura* from *Pleurocera elevatum* and *Cercaria distomatosa* Sonsino.

Cercaria polyadena and *Cercaria isocotylea* are made the basis of the polyadenous cercariae, a new subgroup of the xiphidiocercariae.

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